

Reproductive Biology of *Hemiramphus brasiliensis* and *H. balao* (Hemiramphidae): Maturation, Spawning Frequency, and Fecundity

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Abstract. Analyses of life-history data show that both the size-specific batch fecundities and the age-specific spawning frequencies differ for two halfbeak species, *Hemiramphus brasiliensis*, the ballyhoo, and *H. balao*, the balao. Halfbeak ages were determined from sectioned otoliths; histological data was used to describe oocyte development and estimate spawning frequency; and batch fecundity was measured from counts of whole oocytes in final maturation. *Hemiramphus brasiliensis* lived longer (4 versus 2 years) and had a higher survival rate (14.9% versus 7.5% annually) than *H. balao* did. Of the two species the larger and longer-lived congener, *H. brasiliensis*, reached sexual maturity at a larger size (fork length 198 versus 160 mm). The spawning period of age-0 females was strongly related to season, whereas spawning by older females occurred throughout the year. Reproduction by both species peaked during late spring or early summer, and all mature females were spawning daily during April (*H. brasiliensis*) or June (*H. balao*). This is the first demonstration of iteroparity for the family Hemiramphidae. *H. brasiliensis* had a lower batch fecundity (about 1164 versus 3743 hydrated oocytes for a 100-g female) than *H. balao* did. Such low batch fecundities are typical of the order Beloniformes, but quite different from those of other fishes that live in association with coral reef habitats. *H. balao*'s higher batch fecundity is consistent with the life-history theory that predicts higher numbers of eggs for shorter-lived species; this is possible because *H. balao* produces smaller hydrated oocytes than *H. brasiliensis* (modal diameter about 1.6 versus 2.4 mm). The high spawning frequency of *Hemiramphus* species compensates

for their low batch fecundity. The annual fecundity of both species is similar to that of other reef fish species, after adjusting for body size and spawning frequency. The lifetime fecundity of *H. balao* was very similar to that of *H. brasiliensis*, after accounting for the differences in survival for each species. This suggests a fine tuning of different reproductive traits over the entire life cycle that results in roughly equivalent lifetime fecundity for both species.

Introduction

Two pelagic halfbeak species, *Hemiramphus brasiliensis* and *H. balao*, are conspicuous and abundant elements of the Atlantic Ocean's coral reef fauna (Collette, 1965; Nybakken, 1997, p. 368; McBride *et al.*, 2003). These congeners are similar in size and shape (about 30 cm maximum length; McBride *et al.*, 1996) but differ in both habitat use and diet. Both halfbeak species intermingle above coral reef habitats; otherwise, *H. brasiliensis* is found only inshore of reef habitats and *H. balao* is found only offshore of reefs (McBride *et al.*, 2003). *H. brasiliensis* preys on zooplankton and grazes on seagrasses, whereas *H. balao* is a planktivore (Berkeley and Houde, 1978). Berkeley and Houde (1978) also characterized both species as oviparous summer-spawners with low batch fecundities (*i.e.*, the number of eggs released per spawning event; Hunter *et al.*, 1985), and they reported that *H. brasiliensis* lived longer but had a lower batch fecundity than *H. balao*. These life-history patterns (*i.e.*, age, reproduction, and mortality) are particularly intriguing because such patterns suggest a trade-off between survival and reproductive output.

Comparing life-history traits within species and between morphologically similar species in different habitats is a powerful method for understanding life-history evolution

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(Partridge and Harvey, 1988). If the life-history patterns of fishes evolve largely in response to their environment, it is striking that *H. brasiliensis* and *H. balao* have much larger eggs but lower batch fecundities (*i.e.*, egg diameter >1 mm and thousands of eggs per batch; Berkeley and Houde, 1978) than other coral reef fishes (*e.g.*, see Thresher, 1984). These large eggs and low batch-fecundity values may simply reflect the evolutionary history of hemiramphids. Average batch fecundities for other oviparous hemiramphids range from one hundred (Silva and Davies, 1988; Coates and Van Zwieten, 1992) to a few thousand eggs per female (Talwar, 1962, 1967). In contrast, an average female coral reef fish with a body size similar to that of a *Hemiramphus* species produces about 100,000 eggs (Thresher, 1984). Such low fecundities for *Hemiramphus* species imply either high fertilization success, high survival rates, or the production of multiple batches of eggs. Multiple spawning is a common life-history trait among marine fishes and can greatly increase lifetime reproductive output. Although multiple spawning has been suspected to occur in several hemiramphids, it has never been demonstrated conclusively (*e.g.*, Ling, 1958; Talwar, 1967; Coates and Van Zwieten, 1992).

In this study, multiple spawning is demonstrated for both *H. brasiliensis* and *H. balao*, and new measurements are made of other life-history variables, namely age, mortality, size at maturity, egg size, batch fecundity, and spawning frequencies. Such detailed measurements demonstrate the interaction of phenotypic traits that determine fitness in two congeneric hemiramphids. We also compare these traits for *Hemiramphus* species with those of other hemiramphids and other coral reef fish species to evaluate the importance of evolutionary history in constraining allocation of reproductive effort.

Materials and Methods

Fishes were collected in the coastal waters of southeastern Florida (approx. 26.0° N, 80.0° W to 24.5° N, 82.2° W). *Hemiramphus brasiliensis* and *H. balao* were collected together near the surface in association with coral reefs. *H. brasiliensis* alone was collected in other inshore habitats such as bank habitats in nearby Florida Bay, and so it is more numerous in our collections overall. From July 1997 to October 1998, 100 to 200 fish were subsampled, on each of 4 days per month from the catch of commercial fishing operations. Additional specimens were collected independent of the commercial fishery for a target number of 4 additional trips per month and a sample size of 12 fish per trip. Fish were kept on ice and brought to the laboratory for processing. Fish lengths and weights were measured in the laboratory. Fork length (FL) was measured to the nearest millimeter from the tip of the upper jaw to the fork of the tail. Whole body weight was recorded to the nearest 0.1 g.

Ages of halfbeaks were determined by examining annual increments deposited on otoliths. For each trip in the months from July 1997 to June 1998, 12 fish were selected, at random, for aging; their sagittal otoliths were removed and stored dry. A low-speed saw was used to cut multiple 500- μ m-thick sections along the transverse plane through the otolith core. Otoliths were cut only from fish larger than 200 mm in FL, because otoliths of smaller fish are known to be age-0 (Berkeley and Houde, 1978). Sectioned otoliths were mounted to coded glass slides and examined, usually at 40 \times , with reflected light under a dissecting microscope. The annuli were counted as a measure of fish age, in years, by two readers. If the two independent counts did not agree, then a third reading was conducted, with both readers working together. Only 5% of the otoliths were so difficult to evaluate by both readers that they were rejected ($n = 61$). The frequency of annulus formation was confirmed as annual by a marginal increment analysis. In such an analysis, the percentage of age-1 ballyhoo with an opaque margin, which was interpreted as a second annulus, was calculated for each month; monthly frequencies were checked for periodicity of annulus formation.

Annual survival estimates (\hat{S}) for each species were derived using the estimator from Robson and Chapman (1961):

$$\hat{S} = \frac{\sum_{x=0}^k x f_x'}{\left(\sum_{x=0}^k f_x + \sum_{x=0}^k x f_x - 1 \right)},$$

where x is the coded age class (0 = youngest age [in years] fully vulnerable to fishing), f_x is the number of fish per age-class x , and k is the oldest age class observed. The data for this analysis were only from the period October–May, because age-0 fish are not fully vulnerable to the sampling gear during the summer months (Berkeley and Houde, 1978).

Gonads from 12 randomly selected fish in each collection were removed during the period of July 1997 to October 1998 and prepared for histology. Ovarian tissue was initially fixed in 10% buffered formalin; a section of tissue was then transferred to ethanol, embedded in glycol methacrylate, sectioned along the transverse plane, stained with the periodic acid-Schiff (PAS) reaction, iron-hematoxylin, and counterstained with metanil yellow (Quintero-Hunter *et al.*, 1991). Gonads were assigned a stage based on the most advanced stage of oocyte development, namely perinucleolar, cortical alveolar, vitellogenic, nucleus migration, or nucleus breakdown. Cellular atresia such as postovulatory follicles (POF) and PAS-positive melano-macrophage centers were also noted. Characterization of POFs follows the descriptions of Hunter and Maciewicz (1985). Identification of PAS-positive bodies follows the descriptions in Grier and Taylor (1998; pp. 531, 539–540) and McBride *et al.* (2002).

Table 1

Maturity categories for female *Hemiramphus* spp.

Maturity Category	Most Advanced Oocyte Stage	Atresia and POFs ^a
Immature	Perinucleolar stage	Little or no atresia
Maturing	Cortical alveolar (CA)	Little or no atresia
Mature	Vitellogenic or FOM ^b stage	may be POFs; PAS+ bodies ^c
Regressed	Perinucleolar or CA stage	PAS+ bodies ^c

Females were scored according to their most advanced oocyte stage, and past spawning was inferred based on the presence of postovulatory follicles (POFs) and PAS-positive melano-macrophage centers (see text for details). The dashed line separates immature from mature stages, the division used for calculating size at 50% maturity.

^a Postovulatory follicles (POFs) were observed as newly collapsed structures after dusk. They were readily observed for about 24 h, after which they became more compact and darker.

^b Final oocyte maturation (FOM) began with migration of the nucleus, continued with breakdown of the nucleus (=hydration), and ended with ovulation of eggs.

^c PAS-positive (PAS+) melano-macrophage centers appeared as compact, bright purple bodies when our staining technique was used and are similar to yellow or brown bodies when other stains were used.

The presence of vitellogenic oocytes was the primary indication of maturity (Table 1). Vitellogen, a protein secreted by the liver and endocytosed by oocytes, accumulates in yolk globules that appear in the cytoplasm of oocytes during the spawning season (Wallace and Selman, 1978). Mature females with regressed ovaries were distinguished from immature virgin or maturing virgin females by the presence of PAS-positive melano-macrophage centers. Such PAS-positive bodies are involved in focal tissue degradation, and their presence increases during and after gonad regression (Grier and Taylor, 1998). Size at 50% maturity was calculated as the inflection point of a logistic equation modeling the percent frequency of mature females: $maturity = 1/(1 + \exp(-A[FL - B]))$, where A = the instantaneous rate of increase at the origin and B = the inflection point or the point where 50% of the individuals are mature. Model parameters were estimated by the logistic procedure of SAS software (SAS, 1990).

Spawning frequency was estimated by the "post-ovulatory follicle method" of Hunter and Macewicz (1985). We assumed that POFs became indistinguishable from other atretic bodies after about 24 h, so their presence as collapsed structures with identifiable thecal and granulosa layers indicated that an individual female had spawned during the previous day.

Batch fecundities and oocyte diameters were determined from examination of whole oocytes. Batch fecundities were estimated for 41 specimens of *H. brasiliensis* and 3 of *H. balao* collected in March 1997, May 1997, February–April 1998, and March 1999. About 1 g of tissue was removed

from the anterior and posterior sections of the left and right ovaries, blotted dry, and weighed to the nearest 0.001 g. After the tissue was washed, teased apart, and placed in a solution of 33% glycerin:67% water, the number of hydrated oocytes was counted. Batch fecundity was estimated according to the total weight of the ovary, following the methods of Hunter *et al.* (1985). To increase sample size, these data are presented together with data from Berkeley and Houde (1978), who used a similar method for estimating batch fecundity and obtained similar results. Whole oocyte diameters, for at least 300 oocytes per female, were then measured to the nearest micrometer with the aid of a video system and image-analysis software.

Results

Age, growth, and survival

Sectioned otoliths revealed an alternating pattern of opaque and translucent bands (Fig. 1). The darker, translucent areas represented the periods of faster growth during the summer; the whitish, opaque bands reflected the periods of slower growth during the winter. Marginal increment analysis of *Hemiramphus brasiliensis* otoliths showed that a single annulus was formed each year and that annulus formation was complete by June of each year (Fig. 2). Although too few specimens of *H. balao* were available for the marginal increments of this species to be similarly analyzed, we chose June as the biological hatchdate for both species.

Our aging results indicated that *H. brasiliensis* lives longer than *H. balao* (4 versus 2 years; Fig. 3). At a given age, individuals of *H. brasiliensis* were also larger on average than those of *H. balao*, and females of each species were larger than male conspecifics. Of the 1022 specimens of *H. brasiliensis* aged, the largest was 294 mm FL, whereas of the 132 *H. balao* specimens aged, the largest was 251 mm FL. Annual survival of *H. brasiliensis* during the study period averaged 14.9% (95% confidence limits: 12.2%–17.6%) and was double that of *H. balao* (7.5% on average; 2.01%–13.0%, 95% c.i.).

Reproduction

Ovaries of both halfbeak species were composed of two cylindrical lobes, roughly equal in size. During initial maturation of the specimens we examined, and again during spring recrudescence, these lobes increased in girth, developed a pinkish color, and extended anteriorly along the coelomic cavity. Each lobe was a hollow sac with oocytes arranged in lamellae that extended into a central lumen (Fig. 4A–C). Virgin females lacked any PAS-positive melano-macrophage centers and had a thin gonad wall (Fig. 4A, C); mature, regressed females had PAS-positive melano-macrophage centers and a thick gonad wall (Fig. 4B). Oocytes

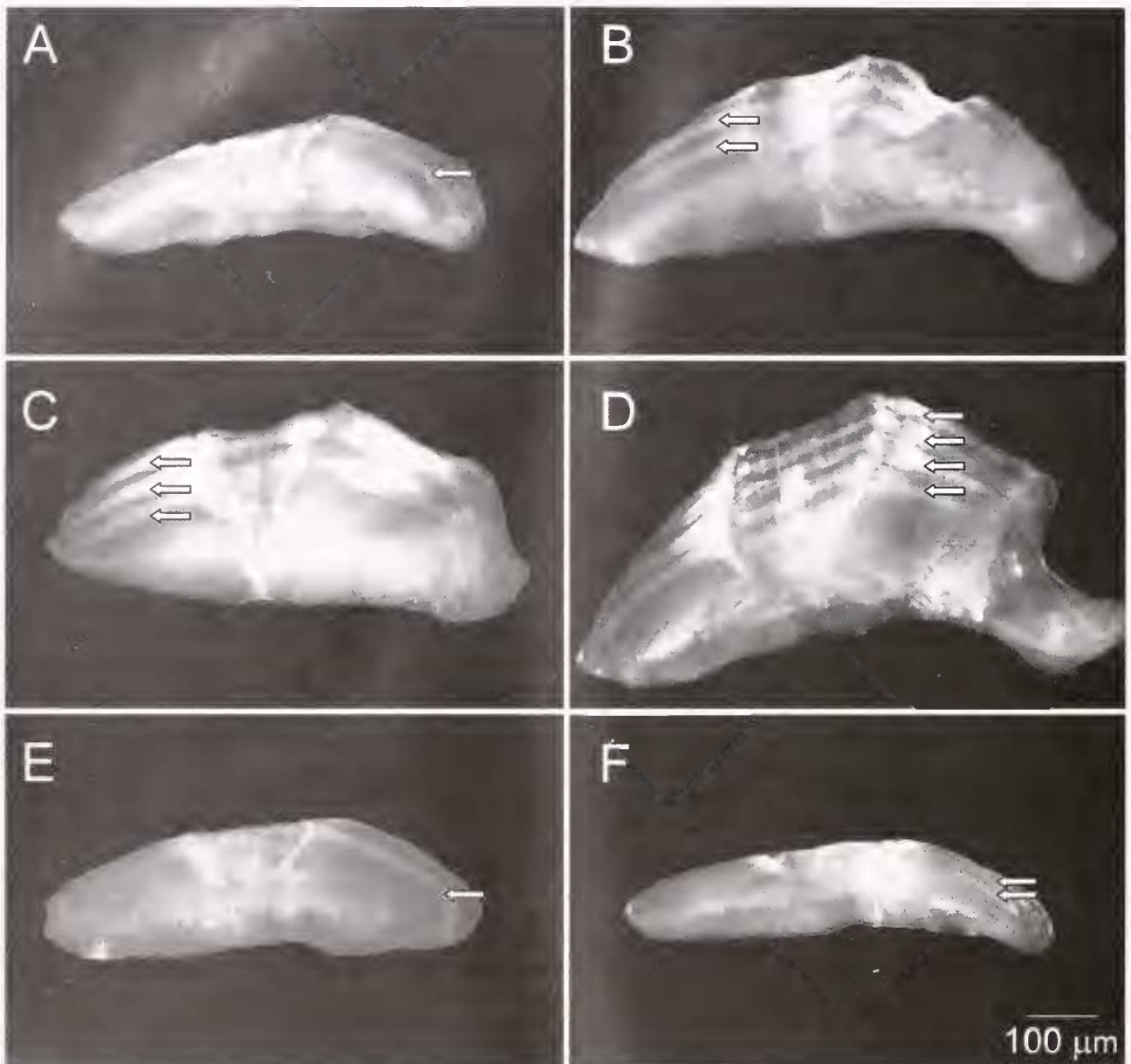


Figure 1. Photomicrographs of sectioned otoliths representing various age classes for *Hemiramphus brasiliensis* (ballyhoo) and *H. balao* (balao). (A) *H. brasiliensis* age-1, (B) *H. brasiliensis* age-2, (C) *H. brasiliensis* age-3, (D) *H. brasiliensis* age-4, (E) *H. balao* age-1, (F) *H. balao* age-2. Arrows indicate annulus locations.

developed in a group-synchronous pattern. Maturing females had oocytes measuring about 200–500 μm in diameter and had cortical alveoli present in the cytoplasm (Fig. 4E). These cortical alveoli appeared as open vacuoles in the cytoplasm, and their color changed from clear (Fig. 4C) to clear with dark specks or purple (Fig. 4D, E) as the oocytes matured. The development of yolk protein, which characterizes a vitellogenic or mature oocyte, was indicated by a red hue in the cytoplasm of oocytes about 400–700 μm in diameter. This yolk protein appeared initially near the nu-

cleus (Fig. 4F, G) but later expanded throughout the cytoplasm and became globular (Fig. 4H). Vitellogenic oocytes with migratory nuclei (*i.e.*, the beginning of final oocyte maturation) always had globular yolk (Fig. 4I, J) and were as small as about 600 μm in diameter. Nucleus migration continued as oocytes enlarged to about 2000 μm in diameter, and the yolk dominated the cytoplasm (Figs. 4K, 5A). Subsequently, the cytoplasm changed from red to pink as the result of hydration, and nucleus breakdown occurred (Figs. 4L, 5B). Ovulating females were collected at dusk.

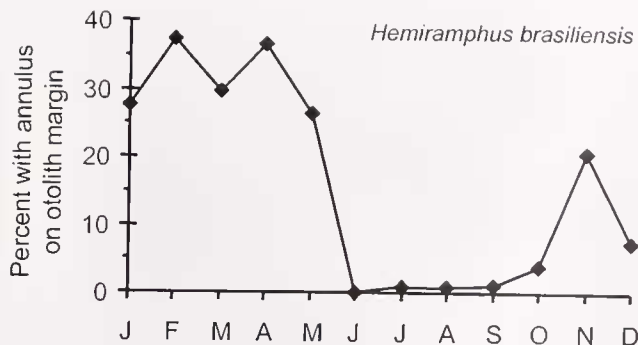


Figure 2. Percent of age-1 *Hemiramphus brasiliensis* (ballyhoo), with a whitish, opaque annulus on the margin of the sectioned otolith, by month. Otoliths were collected from July 1997 to June 1998 ($n = 1019$).

and fresh postovulatory follicles could be observed (Figs. 4J, M; 5C). Vitellogenic oocytes not in the final stages of oocyte maturation were observed together with oocytes that had migrating nuclei and with hydrated oocytes (Fig. 4N), which suggested a fairly rapid turnover of oocytes. The patterns of oocyte development for the two species did not appear to differ, except that the modal diameter of hydrated oocytes was only about 1.6 mm for *H. balao* compared to about 2.4 mm for *H. brasiliensis* (Fig. 5B, D). In addition, females of *H. balao* matured (size at 50% maturity = 160 mm FL) at a smaller size than females of *H. brasiliensis* (i.e., size at 50% maturity = 198 mm FL; Fig. 6). Both species became mature as age-0 fish (i.e., young-of-the-year).

There were distinct seasonal trends in maturation, and the seasonal patterns of POF occurrence indicated prolonged, albeit slightly staggered, spawning periods for both species (Figs. 7, 8). During autumn, the incidence of immature and maturing individuals increased because age-0 fish were more frequently caught in the sampling gear; and the gonads of older fish were regressing as winter approached. Spawning frequency peaked in April for *H. brasiliensis* and in June for *H. balao*, but spawning by some females was evident year-round based on the continued presence of POFs in older fish. Spawning frequencies were clearly age-specific, even for such short-lived species. All age classes of both species were spawning on a daily, or near-daily, basis, during spring or summer (Fig. 8). In other seasons, age-1 females spawned more frequently than age-0 females did, but age-2 ballyhoo females did not necessarily spawn more frequently than age-1 ballyhoo females. In terms of environmental associations, spawning activity peaked when the photoperiod was longest (i.e., June), and most juveniles were growing when temperatures were highest (i.e., August; Fig. 9).

Batch fecundity was higher for *H. balao* than for *H. brasiliensis* across the range of mature sizes (Fig. 10). Batch fecundity also increased more rapidly with increasing fish size in *H. balao* than in *H. brasiliensis*. The average batch

size for a 100-g female of *H. balao* (3743 oocytes) was more than three times that of a 100-g female of *H. brasiliensis* (1164 oocytes). At a common size of 200 g, the batch fecundity of *H. balao* (8346 oocytes) was more than five times that of *H. brasiliensis* (1538 oocytes).

Discussion

We report here, for the first time, the evidence that *Hemiramphus* species are multiple-spawners with group-synchronous oocyte development. Many general life-history patterns are similar for the two species of halfbeak. Both are short-lived, fast-growing, gonochoristic, and oviparous. Still, there were interspecific life-history differences, some of which varied in a manner predicted by life-history theory. The results of this study show the interplay between different phenotype-based life-history traits that are balanced out once lifetime reproductive output is calculated.

Maximum ages for both species in our study were 1 or 2 years older than the ages determined in a previous study, but our results do not alter the conclusions that these are fast-growing and short-lived species (Berkeley and Houde, 1978). Berkeley and Houde (1978) reported that the maximum age of 1100 specimens of *H. brasiliensis* was age-2 and the maximum age of 135 specimens of *H. balao* was age-1. They read annuli on fish scales, and some researchers have noted that this method tends to underestimate ages compared to the use of otoliths (e.g., Lowerre-Barbieri *et al.*, 1994). Our results may also differ by mere chance from

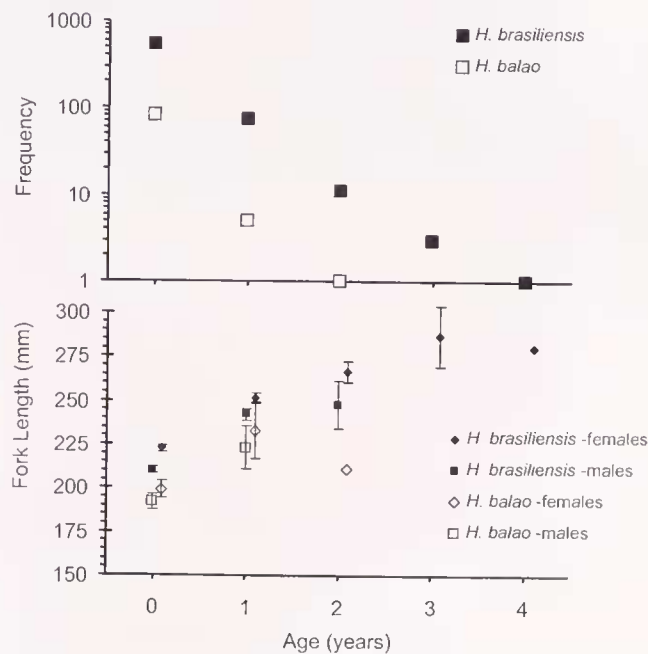


Figure 3. Number of *Hemiramphus brasiliensis* (ballyhoo) and *H. balao* (balao), collected by age class (upper panel) and the sizes of each age class, by species and sex (lower panel; mean \pm 95% confidence limits).

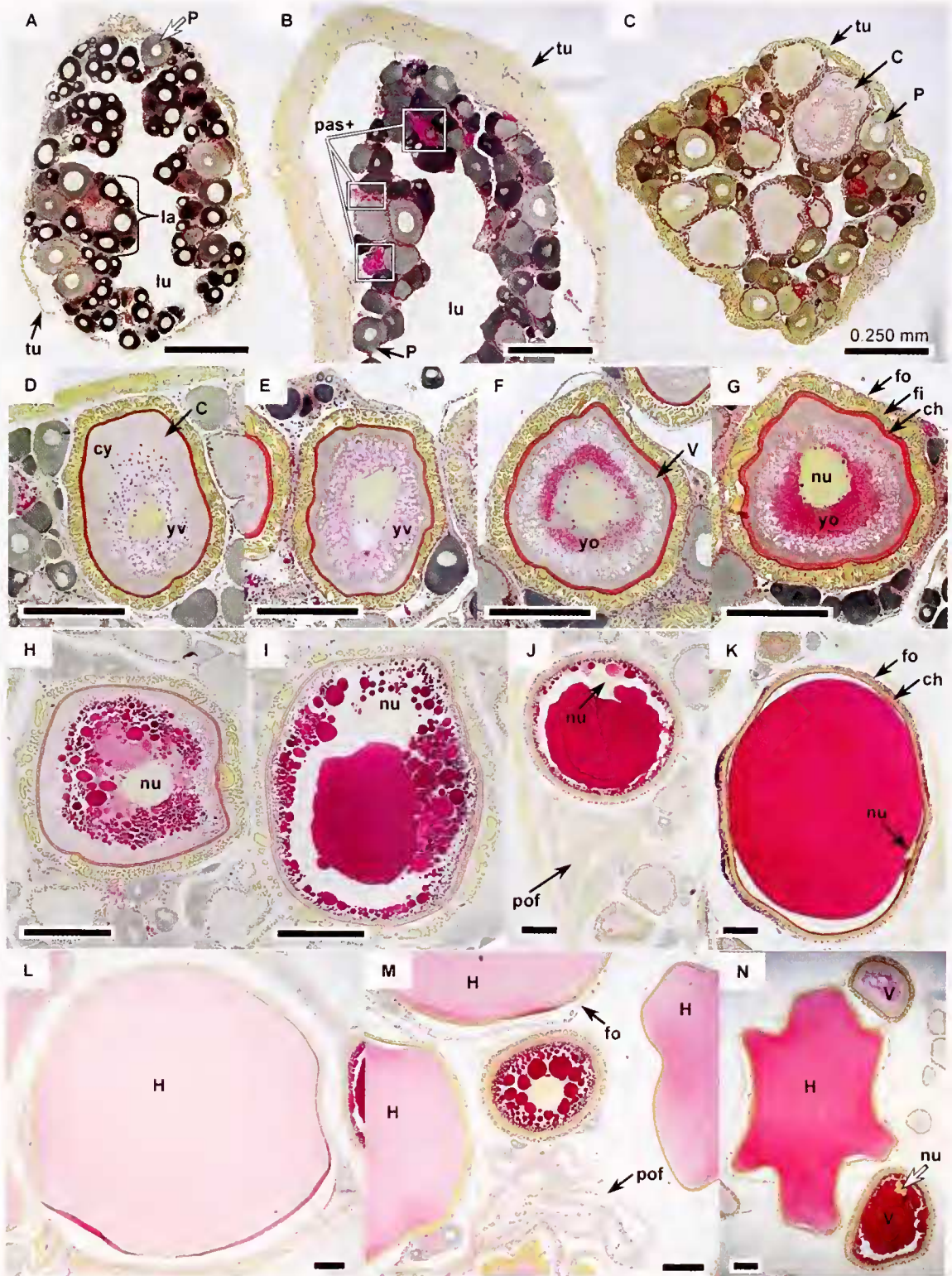


Figure 4. Histological features of ovarian and oocyte development for *Hemiramphus brasiliensis* (bally-hoo). (A) whole cross section from a virgin, immature female; (B) partial cross section from a regressed, mature female; (C) whole cross section from a virgin, maturing female; (D) enlargement of detail of a late-stage "yolk vesicle" oocyte with cortical alveoli; (E) an even later-stage "yolk vesicle" oocyte; (F) a very early-stage "yolked" or vitellogenic oocyte; (G) a slightly more advanced vitellogenic oocyte; (H) a vitellogenic oocyte with yolk globules (probably a cell undergoing nucleus migration); (I) a vitellogenic oocyte with a migrating nucleus,

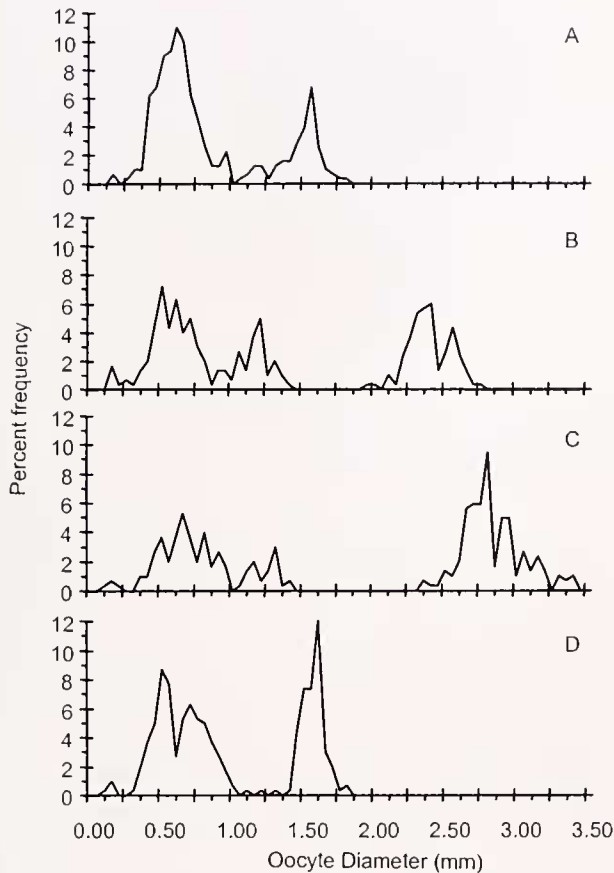


Figure 5. Oocyte diameter frequencies for *Hemiramphus brasiliensis* (ballyhoo) (A-C) and *H. balao* (balao) (D), in the final stages of oocyte maturation. The largest mode in each figure represents a developing batch of oocytes in final oocyte maturation, whereas the smallest mode represents a reservoir of primary growth oocytes and vitellogenic oocytes prior to nucleus migration. A third, middle mode of oocytes represents a batch of oocytes just entering final oocyte maturation. Measurements were made from (A) a mature *H. brasiliensis* whose most advanced oocyte stage was nucleus migration, (B) a hydrated *H. brasiliensis* whose most advanced oocyte stage was nucleus breakdown, (C) a spawning *H. brasiliensis* with ovulated eggs, (D) a hydrated *H. balao* whose most advanced oocyte stage was nucleus breakdown. At least 300 oocytes were measured per female.

those of Berkeley and Houde; for *H. brasiliensis* we found only three age-3 individuals and one age-4; for *H. balao* we found only a single age-2 individual. Sample sizes in both

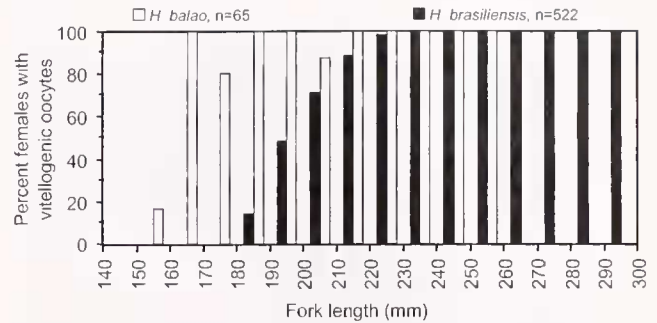


Figure 6. Percent frequency of mature (vitellogenic) female *Hemiramphus brasiliensis* (ballyhoo) and *H. balao* (balao). Values are calculated by fork length intervals of 10 mm from fish collected during the peak spawning season (March-August). n = number of fish.

studies were larger for *H. brasiliensis* because this species is more commonly caught and is found in a wider range of habitats than *H. balao* (McBride *et al.*, 2003). At least one other hemiramphid, *Reporhamphus melanochir*, lives longer and grows larger (7 years, 380-mm FL; Ling, 1958). So even among hemiramphids, *H. brasiliensis* and *H. balao* are short-lived and grow to only modest lengths.

Sizes of age-1 fish (mean = 248-mm FL for *H. brasiliensis* and 226-mm FL for *H. balao*) were significantly different for the two species and were generally larger than previously reported. Berkeley and Houde (1978) reported that size at age-1 can vary between years for *H. brasiliensis* (1974 = 216-mm FL, 1975 = 230-mm FL) and that at age-1, *H. balao* was smaller (209-mm FL) than *H. brasiliensis*. The sizes of both species overlapped (McBride *et al.*, 1996), and the mean sizes may vary from year to year naturally. Efforts to estimate the growth rates by nonlinear models failed because the short life spans of both species made it impossible to reasonably fit a growth model to the data. *H. brasiliensis*, however, spawns about 2 months earlier than *H. balao* (*i.e.*, April *versus* June modes), so their growth rates may be fairly similar on a daily or monthly basis. We also found, as did Berkeley and Houde (1978), that females were longer than males at a common age.

Survival rates differed between the two species. In our study, *H. brasiliensis* had a higher annual survival rate than *H. balao* did: 14.9% and 7.5%, respectively. We found the

indicating the beginning of final oocyte maturation; (J) a vitellogenic oocyte with a migrating nucleus next to a fresh postovulatory follicle (POF); (K) a late-stage vitellogenic oocyte with the nucleus positioned against the chorion; (L) a fully hydrated oocyte after nucleus breakdown; (M) three hydrated oocytes, one without a follicle and adjacent to a fresh POF; and (N) juxtaposition of a vitellogenic oocyte prior to nucleus migration, a vitellogenic oocyte undergoing nucleus migration, and a hydrated oocyte following nucleus breakdown. The major stages of oocyte development are indicated by capitalized letters: Perinucleolar (P), cortical alveolar (C) (=yolk vesicle), vitellogenic (V) (=yolked), hydrated (H). Other features include the chorion (ch), cytoplasm (cy), fibrils (fi), follicle (fo), lamellae (la), lumen (lu), nucleus (nu), periodic acid-Schiff reaction-positive (pas+) melano-macrophage centers, post-ovulatory follicle (pof), tunic (tu) (=gonad wall), yolk formation (yo), and yolk vesicles (yv). All scale bars, 0.250 mm.

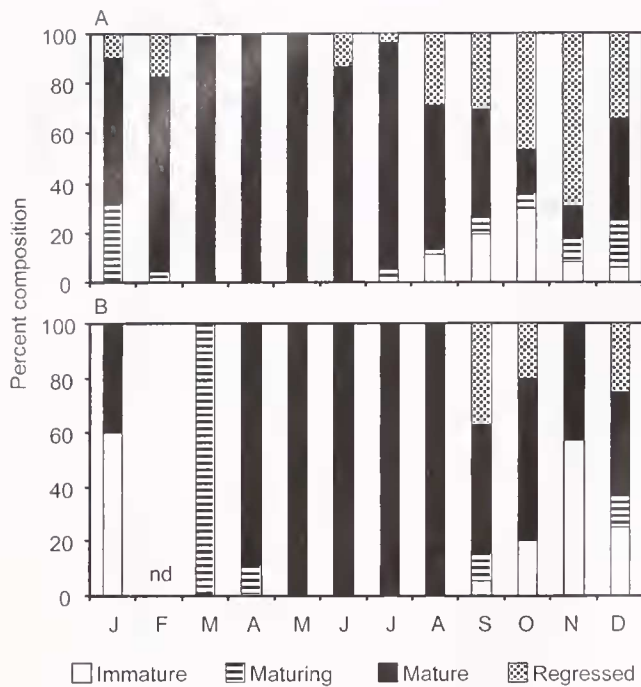


Figure 7. Seasonal reproductive cycles of (A) female *Hemiramphus brasiliensis* (ballyboo) and (B) female *H. balao*, (balao) based on histological criteria for fish collected from July 1997 to October 1998. Values were calculated from mature fish sizes only (fork length ≥ 198 mm for *H. brasiliensis* and ≥ 160 mm for *H. balao*). Nd = no data.

same pattern when we calculated survival rates using data from Berkeley and Houde (1978), the only previous study available: estimates of *H. brasiliensis* survival varied between the collection years (1974 = 23.8%, 1975 = 17.3%); these values were higher than that for *H. balao* (1974 = 12.4%). Even if the use of scales by Berkeley and Houde resulted in truncated ages (not identifying fish older than age-2), the number of fish aged was so large that the estimates of survival should not have been biased (Murphy, 1997). The more likely cause of the interannual variation is that survival rates may have declined since the mid-1970s or that violations of steady-state assumptions (variable recruitment of age-0 fish) may have biased the estimates of annual survival as calculated here.

The macroscopic appearance and development of *Hemiramphus* species gonads were similar to those of *Hyporhamphus* (*Reporhamphus*) *melanochir* (Ling, 1958). The group-synchronous nature of oocyte development and large egg sizes have been noted for other hemiramphids (Ling, 1958; Talwar, 1967). The pattern of final oocyte maturation follows the diel cycle, and both species spawn at dusk (McBride *et al.*, 2003). At sunset, the modal diameter of ovulated *H. brasiliensis* eggs was 2.8 mm. Berkeley and Houde (1978) illustrated an *H. brasiliensis* embryo that was about 2.5 mm in diameter and a near-hydrated oocyte that

was 2.2 mm. The modal size of hydrated *H. balao* oocytes (1.6 mm) was also very close to the size of the *H. balao* egg (1.5 mm) illustrated by Rass (1972). These independent descriptions and illustrations of mature oocytes and eggs confirm that interspecific differences in egg sizes exist for these two congeners.

Sizes at maturity for both species were smaller than sizes attained by the first winter, and we agree with Berkeley and Houde (1978) that both species mature in their first year. In our study, the size at 50% maturity was 63.3% of the maximum body size for *H. brasiliensis* (313 mm FL) and 58.6% for *H. balao* (273 mm FL; McBride *et al.*, 1996). To our knowledge, no study of hemiramphids has determined size at maturity with the precision that we achieved here, but other studies have reported the size of the smallest females with hydrated oocytes. Size at maturity in these other species is 56.8% maximum body length for *Hyporhamphus melanochir* (Ling, 1958), 58.2% for *Hemiramphus limbatus* (Silva and Davies, 1988), and 58.0% for *Zenarchopterus kampeni* (Coates and Van Zwieten, 1992). Size at maturity is very close to 60% maximum body size for a number of hemiramphids, and this percentage value may be useful for predicting the size at maturity of hemiramphid that have not been studied.

Both *H. brasiliensis* and *H. balao* spawn frequently, even daily, for at least a few months of the year. Although a

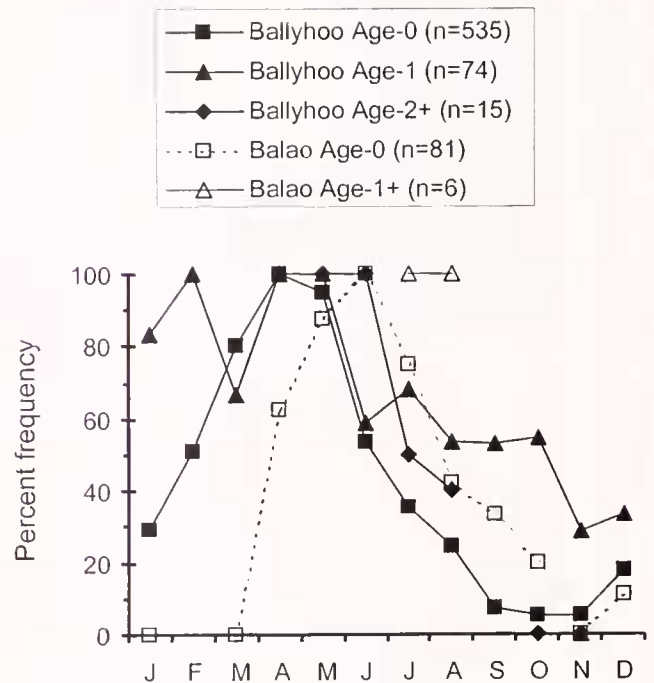


Figure 8. Average spawning frequency for *Hemiramphus brasiliensis* (ballyboo), and *H. balao* (balao), by age class. Spawning frequency is based on the percent frequency of females with fresh postovulatory follicles (POFs). A value of 100% means that all females in a particular age class were spawning every day of that month. n = number of fish.

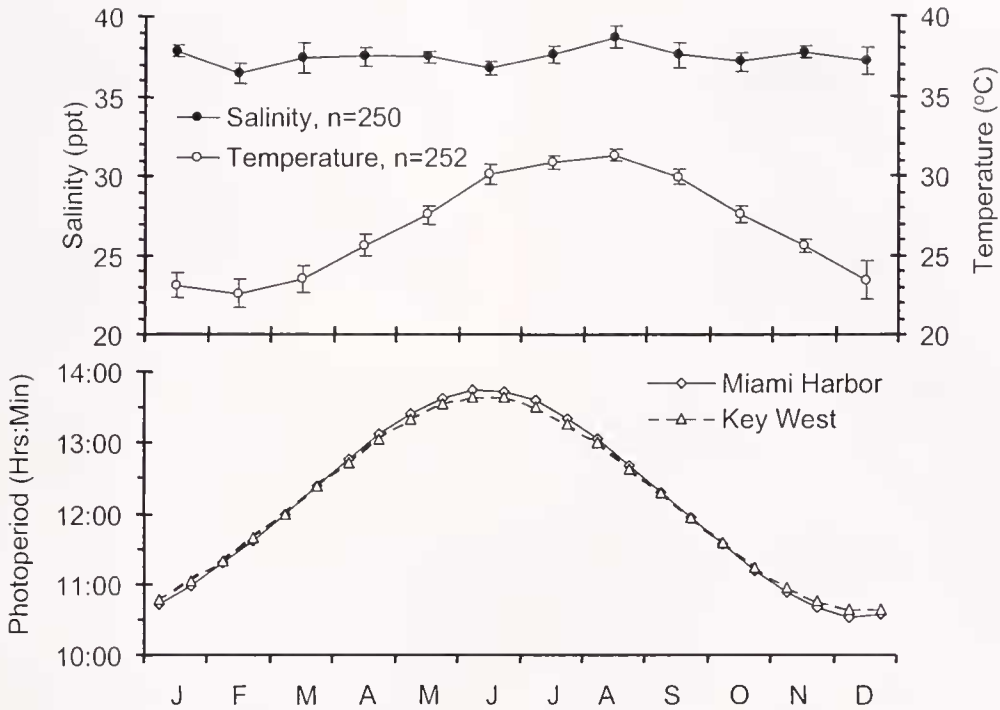


Figure 9. Monthly average salinity and temperature (upper panel) measured at the sea surface at the time of fish collection. Error bars are 95% confidence limits. Seasonal change in photoperiod for Miami Harbor entrance and Key West (lower panel; data source: National Oceanic and Atmospheric Administration Tide Tables).

prolonged reproductive season has been noted for other hemiramphids (Ling, 1958; Coates and Van Zwieten, 1992), this study provides the first conclusive evidence of multiple

spawning within a year for any hemiramphid. Moreover, our age-specific analysis demonstrates that older fish spawn more frequently and for longer periods than age-0 fish do. In

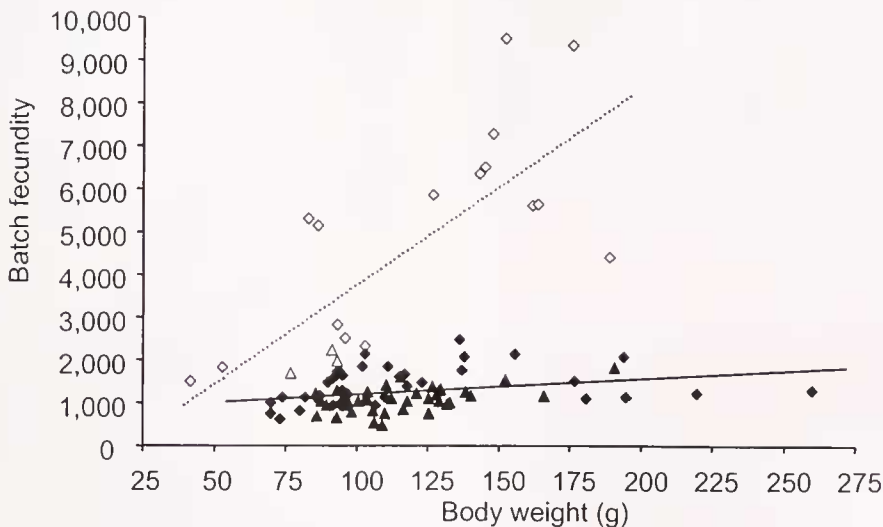


Figure 10. Batch fecundity for female *Hemiramphus brasiliensis* (ballyhoo) (filled symbols) and *H. balao* (balao) (open symbols), as related to fish size. Data from Berkeley and Houde (1978) are included (diamond symbols), together with data from this study (triangles), to show overlap of values and to increase sample size. Batch fecundity for *H. brasiliensis* was not significantly correlated with fish size ($Y = 790.57 + [3.7411 * X]$, $r^2 = 0.11$, $n = 74$), but batch fecundity for *H. balao* was significantly correlated with fish size ($Y = 858.79 + [46.024 * X]$, $r^2 = 0.56$, $n = 20$).

Table 2

A matrix approach to estimate the expected lifetime fecundity of two species of *Hemiramphus* as the average number of eggs produced in the next generation by each female in the present generation

Species	x (years)	l_x	d_x	f_x	w_x	m_x	$l_x m_x$
<i>H. brasiliensis</i>	0	1.00000	151	1117.3	87.3	168,719	168,719
	1	0.14870	240	1264.6	126.7	303,507	45,133
	2	0.02211	240	1353.2	150.4	324,757	7,181
	3	0.00329	240	1493.4	187.9	358,419	1,179
	4	0.00049	240	1445.0	174.9	346,809	170
						$\Sigma l_x m_x = 222,381$	
<i>H. balao</i>	0	1.00000	129	2124.91	64.8	274,114	274,114
	1	0.07527	240	4226.33	110.5	1,014,319	76,347
	2	0.00567	240	2787.75	79.2	669,060	3,791
						$\Sigma l_x m_x = 354,251$	

Variables are calculated by age classes in years (x). Survival by age class (l_x) was determined by the results of the Robson-Chapman survival estimate (see text for details). The number of days spawning by age class (d_x) was generalized from Figure 8. The batch fecundity by the average size female in each age class (f_x) was estimated from Figure 10, and the average weight of females in each age class (w_x) was calculated from length-weight relationships (McBride, unpubl.). Annual fecundity by age class (m_x) is the product of the spawning frequency (d_x) and batch fecundity (f_x), and the expected reproductive output ($l_x m_x$) is the expected contribution of eggs produced by each age class after accounting for survival.

fact, histological examination shows that some spawning by *H. brasiliensis* occurred year-round.

Altogether, our data demonstrate that *H. balao* is a smaller, shorter-lived fish than *H. brasiliensis*, but it matures at a smaller size and produces more, albeit smaller, eggs per batch. Morphological constraints of body size probably lead to this inverse relationship between size and number of eggs produced per spawning event (Elgar, 1990), and the larger batch size of *H. balao* is consistent with the life-history theory that predicts larger batch size for shorter-lived species (Stearns, 1976). *H. balao* is also more common offshore of the reef tract, where food may be patchier than it is inshore; and various models predict that this would select for more numerous but smaller eggs (Wootton, 1994). Ultimately, the life-history traits that typically represent trade-offs in evolutionary terms (*i.e.*, survival and growth rates, age-specific spawning frequency, size-specific batch fecundity) are balanced so that the lifetime egg production of both *Hemiramphus* species is the same order of magnitude; Table 2).

Certainly the environment is shaping some elements of the reproductive traits of these *Hemiramphus* species, but the influence of their phylogenetic history is clearly evident. Although *Hemiramphus* species are not structure-oriented, they are associated with coral reef habitat and thus are exposed to environmental cues similar to those encountered by coral reef fish. (*e.g.*, warm temperature, high salinity, open coastal hydrodynamics, and tropical weather disturbances). However, compared to most marine teleosts, and particularly other coral reef fishes, *H. brasiliensis* and *H. balao* both have very large eggs, high spawning frequencies, and low batch fecundities (*e.g.*, Thresher, 1984; Gross,

1987). Their reproductive style is typical of the order Belontiiformes, with its large eggs, low fecundity, multiple spawning events, and embryos that attach to floating vegetation (Berkeley and Houde, 1978; Collette *et al.*, 1984). In fact, Hemiramphidae is a particularly interesting family to study while exploring trade-offs in reproductive traits because there is remarkable variation in the egg size, fecundity, and reproductive mode of its species. For example, the diameters of hemiramphid eggs range from 1.3 to 3.5 mm, and reproductive modes include producing demersal eggs, buoyant pelagic eggs, or precocious young (Wourms, 1981; Collette *et al.*, 1984; Meisner and Burns, 1997).

Although many of the life-history traits of *H. brasiliensis* and *H. balao* are not shared by other coral reef fishes that have similar habitats, the annual fecundities of these two species might well be in line with those of other coral reef fishes. To illustrate this point, annual individual fecundities of *H. brasiliensis* and *H. balao* range from 169,000 to 1,014,000 eggs per year (Table 2), and these estimates are within the range of annual fecundity for a relatively small lutjanid, *Rhomboplites aurorubens* (140,000–3,000,000 eggs; Cuellar *et al.*, 1996). Although the maximum fecundity of *R. aurorubens* is considerably higher than that estimated for halfbeaks, *R. aurorubens* spawns at larger sizes than the two *Hemiramphus* species do (approx. range: 100–700 g; Cuellar *et al.*, 1996).

We conclude that once adjustments are made for their size, *H. brasiliensis* and *H. balao* do not have low annual or lifetime fecundities, when compared either to other hemiramphids or to other coral reef fishes. This descriptive study of hemiramphid life-history patterns suggests that consideration of atypical but reef-associated species, such as half-

beaks, in future ecological and evolutionary analyses can improve our understanding of adaptation and community dynamics of coastal fishes. Moreover, the special traits in the early life history of *H. brasiliensis* and *H. balao*, such as large eggs that are attached to floating vegetation near the surface, should be considered in the development of larval dispersal models so that the variable responses of fishes to environmental and anthropogenic processes can be more completely understood (e.g., Roberts, 1997; Cowen *et al.*, 2000).

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